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Use of a mathematical model to describe the epidemiology of *Lepeophtheirus salmonis* on farmed Atlantic salmon *Salmo salar* in the Hardangerfjord, Norway

George Gettinby [a], Chris Robbins [b], Fiona Lees [a], Peter A. Heuch [c], Bengt Finstad [d], Ragnild Malkenes [e], Crawford W. Revie [f,]*

[a] *Mathematics and Statistics, University of Strathclyde, Richmond Street, Glasgow G1 1XH, UK*
[b] *Grallator, 8 Chendre Close, Hayfield, High Peak, Derbyshire SK22 2PH, UK*
[c] *National Veterinary Institute, Oslo, Norway*
[d] *Norwegian Institute for Nature Research, Trondheim, Norway*
[e] *Hardanger Fish Health Network, Tysnes, Norway*
[f] *Atlantic Veterinary College, University of PEI, Charlottetown, PE C1A 8A5, Canada*

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ABSTRACT

Infestation patterns of the sea louse *Lepeophtheirus salmonis* from 44 salmon farms in the Hardangerfjord on the south-west coast of Norway over the period 2004 to 2007 were assimilated to create 20-month production cycle profiles for spring and autumn stocked generations. The timing and frequency of in-feed and bath treatments to control sea lice associated with these profiles was considered. Spring and autumn stocked farms were observed to have different patterns of sea lice counts on salmon during the first and second years of production. Spring stocked sites experienced increasing infestation toward the end of the first year and on average counts remained elevated thereafter, whereas autumn stocked sites averaged lower sea lice counts throughout most of the production cycle until the latter part of the second year when these escalated rapidly. In-feed treatments were the predominant form of sea lice control in the first half of the production cycle on spring stocked farms, whereas bath treatments were used exclusively in the second half of the production cycle; a very similar pattern of therapeutant use was observed on autumn stocked farms.

Results using the *SLiDESim* (**S**ea **Li**ce **D**ifference **E**quation **Sim**ulation) infection model and a range of biological and production parameters showed that modelling resulted in a better fit to the mobile lice profiles for autumn stocked farms compared to spring stocked farms. Some features of the mobile lice profiles were not captured by the infection model such as the oscillation of the population between months 11 and 18 of the production cycle on spring stocked farms, and a large peak observed in month 19 on autumn stocked farms. Before modelling can be used to evaluate optimal treatment strategies or other management interventions there remains a need to more clearly understand the underlying biological processes associated with the dynamics of sea lice infestations in the Hardangerfjord.

1. Introduction

Sea lice infections are a serious worldwide threat to indigenous wild salmon populations and the sustainability of farmed salmon production units (Krkošek et al., 2007; Costello, 2009). In recent years the control of lice in European and North and South American salmon producing countries has become critical with many countries adopting strategic regional sea lice control programmes (Heuch et al., 2005; Revie et al., 2009). Not only can lice have a negative impact on farmed fish, in terms of product quality and farm productivity, but increasingly lice infected salmon farms may be a source of *Lepeophtheirus salmonis* infestation for wild salmon populations (Bjørn et al., 2001; Krkošek et al., 2007; Marty et al., 2010). In particular, young sea-faring wild salmon and sea trout may be exposed to sea lice sources from fish farms (Gargan et al., 2003; Heuch et al., 2005). Over the past decade salmon farms in Northern Europe and Chile have relied on a range of veterinary medicines, applied as in-feed or bath treatments, to control lice infestation levels (Sevatdal et al., 2005; Lees et al., 2008a). This has successfully driven down infections on farmed salmon populations with many control programmes achieving a low prevalence of infestation and lice abundances of less than one adult female per fish (Heuch et al., 2009; Heuch et al., 2011-this issue). The use of such medicines is not only expensive but comes with environmental concerns, as well as increasing evidence that lice populations are becoming tolerant to such treatments (Denholm et al., 2002; Fallang et al., 2004; Sevatdal et al., 2005; Bravo et al., 2008; Lees et al., 2008b). There is a need to better understand the epidemiology of lice infections on farms and to conserve the use of medicines if they are

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* Corresponding author at: Department of Health Management, Atlantic Veterinary College, University of Prince Edward Island, 550 University Ave, Charlottetown, PE, C1A 4P3, Canada. Tel.: +1 902 620 5062; fax: +1 902 620 5053.
E-mail address: crevie@upei.ca (C.W. Revie).

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to remain effective (Fallang et al., 2005; Lees et al., 2008c; Westcott et al., 2008).

Over the past decade mathematical modelling has increasingly been used as a means to better understand the transmission of aquatic pathogens (Reno, 1998; McCallum et al., 2004; Murray, 2009; Green, 2010). Work in this area has included the consideration of sea lice population dynamics. A number of studies have focused on potential interactions between sea lice from wild and farmed sources (Murray and Gillibrand, 2006; Krkošek et al., 2006; Foreman et al., 2009), while a few have specifically modelled the biological development of lice populations in laboratory (Tucker et al., 2002; Stien et al., 2005) or field (Revie et al., 2005; Krkošek et al., 2009) settings.

The Hardangerfjord in the south-west of Norway supports a large number of production units and is an important salmon producing area where coordinated sea lice control is widely practised (Heuch et al., 2009). A three year Hardangerfjord project was initiated in 2004 to better understand the dynamics of sea lice populations over a wide area. By 2007 a large body of data had become available on sea lice populations from different salmon farms and how these populations were being controlled (Heuch et al., 2009). This communication reports on the epidemiological patterns of infection found on farms in the Hardangerfjord and explores the adaptation of a mathematical population model to explore the interaction between *L. salmonis* infections and treatment during spring and autumn stocked production cycles.

2. Materials and methods

2.1. Hardangerfjord lice infection data

The Hardanger Fish Health Network (HFN) has operated since 2004 in the Hardangerfjord on the south-west coast of Norway where there is a high density of salmon farms. This network was a key partner in the Hardangerfjord Salmon Lice Project which had the overall goal of understanding the complex interaction of hosts, parasites, environment and fish farms (Heuch et al., 2009).[1] In total 16 of the 18 fish farming companies, controlling around 95% of the farmed fish population in the fjord, participated in the project with an aim of keeping mean lice abundance below agreed levels, particularly during the wild smolt run in May.

Throughout each production cycle, farms in the Hardangerfjord provided stocking information, together with sea lice counts and treatment data to the HFN. Sea lice counts were collected according to guidelines provided in standard sampling protocols. This enabled abundance, measured as the mean number of lice found on sampled fish (Bush et al., 1997), and sea lice treatment interventions to be monitored across the fjord on a continuous basis. In addition dedicated counting teams collected detailed counts of lice on farmed fish between April and September each year. Data supplied to the HFN by each farm were cross-checked against data collected by the counting teams. Where discrepancies arose, farms were asked by the HFN to check their own records and the correct information was identified. Farm stocking, lice counts and treatment data were available for 69 salmon farms in the Hardangerfjord between 2004 and 2007, although not all farms were stocked every year.

The data were analysed to create a profile of lice abundance and treatment on every farm throughout each production cycle. Most farms practised a single year class stocking pattern with either spring or autumn stocking, followed by a fallowing period. Two characteristic sea lice infestation profiles were developed; one for sites that stocked in the spring and one for sites that stocked in the autumn. Mixed year class production cycles, and those where it was not possible to determine the year class of the smolts, were discounted for the purpose of creating these profiles.

It has previously been shown that salmon farms in the inner fjord generally have a lower abundance of salmon lice (Heuch et al., 2009). In the data set under consideration in this study a majority of sites were located in the inner fjord area for both the spring and autumn stocked groups, though the percentage of inner fjord sites (70%; 19 of N = 27) in the spring group was higher than was the case for the autumn stocked group (54%; 13 of N = 24).

2.2. SLiDESim model for lice infections

The *SLiDESim* (**S**ea **Li**ce **D**ifference **E**quation **Sim**ulation) infection model is based on a mathematical representation of *L. salmonis* populations on farmed fish. Its application to lice infestation on Scottish farms has been described in detail by Revie et al. (2005). The model consists of six compartmental "stages". The first compartment/stage includes the egg and the two planktonic stages. From this first compartment lice move to the infective copepodid and chalimus I–IV compartmental stage. Following varying periods of biological development lice leave the chalimus compartment and develop to the pre-adult and then to the adult compartmental stages. A separate compartmental stage is assigned to gravid females as this gives rise to the egg and planktonic stages and completes the life-cycle. An external compartmental stage is included to represent the flow of external copepodids which migrate in to the infective copepodid/chalimus compartmental stage of the life-cycle model. This external infective pressure is necessary to initiate infection on fish and to represent on-going external infestation pressure from sources such as neighbouring farms or wild salmonids. Each compartment represents lice abundance and is modelled using a delay differential equation to ensure that population stages take account of the different biological development times. The key mathematical equations for the life cycle between the infective copepodid, chalimus, pre-adult and gravid female stages follow from those given in Revie et al. (2005)

$$\frac{dL_1(t)}{dt} = F(t) - F(t-\tau_1)e^{-b_1\tau_1} - b_1(t)L_1(t)$$

$$\frac{dL_2(t)}{dt} = \eta F(t-\tau_1)e^{-b_1\tau_1} - \eta F(t-\tau_1-\tau_2)e^{-b_1\tau_1-b_2\tau_2} - b_2(t)L_2(t)$$

$$\begin{aligned}\frac{dL_3(t)}{dt} &= \eta F(t-\tau_1-\tau_2)e^{-b_1\tau_1-b_2\tau_2} \\ &\quad - \eta F(t-\tau_1-\tau_2-\tau_3)e^{-b_1\tau_1-b_2\tau_2-b_3\tau_3} - b_3(t)L_3(t)\end{aligned}$$

$$\frac{dL_4(t)}{dt} = \eta F(t-\tau_1-\tau_2-\tau_3)e^{-b_1\tau_1-b_2\tau_2-b_3\tau_3} - b_4(t)L_4(t)$$

where L_1, L_2, L_3 and L_4 are the number of lice per fish in the chalimus, pre-adult female, adult female and gravid female stages respectively; T_1, T_2 and T_3 are the times spent in the chalimus, pre-adult and adult stages respectively; b_1, b_2, b_3 and b_4 are the mortality rates in the chalimus, pre-adult, adult female and gravid female stages respectively; F represents the population feedback and external infection pressure; and η is the fraction of the chalimus population that develop into females.

The average periods of development for chalimus, pre-adult, adult and egg to chalimus used in the model were 15, 20, 10 and 20 days respectively, based on mean water temperature (Tucker et al., 2000). A 50:50 ratio of female to male adults was adopted and gravid females were assumed to exponentially decline with a half-life of 12 days. It is recognised that laboratory studies indicate development rates to be affected by temperature and a theoretical outline indicating how such variability could be modelled has been proposed (Stien et al., 2005). However, previous investigations using the model and including

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[1] See also http://www.nina.no/Aktuelt/Artikkel/tabid/945/smid/873/ArticleID/422/Default.aspx.